Potential effects of ocean acidification on the California Current food web and fisheries: ecosystem model projections

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Abstract:	The benefits and ecosystem services that humans derive from the oceans are threatened by numerous global change stressors, one of which is ocean acidification. Here, we describe the effects of ocean acidification on an upwelling system that already experiences inherently low pH conditions, the California Current. We used an end-to-end ecosystem model (Atlantis), forced by downscaled global climate models and informed by a meta-analysis of the pH sensitivities of local taxa, to investigate the direct and indirect effects of future pH on biomass and fisheries revenues. Our model projects a 0.2 unit drop in pH during the summer upwelling season, which results in wide-ranging magnitudes of effects across guilds and functional groups. The most dramatic direct effects of future pH may be expected on epibenthic invertebrates, and strong indirect effects expected on demersal fish, sharks, and epibenthic invertebrates because they consume species sensitive to changing pH. The model's pelagic community, including marine mammals and seabirds, was much less influenced by future pH. Some functional groups were less sensitive to changing pH in the model than might be expected from experimental studies in the empirical literature due to high population productivity (e.g. copepods, pteropods, Dungeness

crabs). Model results suggest strong effects of reduced pH on nearshore state-managed invertebrate fisheries but modest effects on the groundfish fishery. Our results provide a set of projections that generally support and build upon previous findings and set the stage for hypotheses to guide future modeling and experimental analysis on the effects of OA on marine ecosystems and fisheries.

1 **Title:** Potential effects of ocean acidification on the California Current food web and
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27 **Running title:** Potential effects of ocean acidification in the California Current

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Abstract

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by numerous global change stressors, one of which is ocean acidification. Here, we

describe the effects of ocean acidification on an upwelling system that already

experiences inherently low pH conditions, the California Current. We used an end-to-end

ecosystem model (Atlantis), forced by downscaled global climate models and informed

by a meta-analysis of the pH sensitivities of local taxa, to investigate the direct and

indirect effects of future pH on biomass and fisheries revenues. Our model projects a 0.2

unit drop in pH during the summer upwelling season, which results in wide-ranging

magnitudes of effects across guilds and functional groups. The most dramatic direct

effects of future pH may be expected on epibenthic invertebrates, and strong indirect

effects expected on demersal fish, sharks, and epibenthic invertebrates because they

consume species sensitive to changing pH. The model's pelagic community, including

marine mammals and seabirds, was much less influenced by future pH. Some functional

groups were less sensitive to changing pH in the model than might be expected from

experimental studies in the empirical literature due to high population productivity (e.g.

copepods, pteropods, Dungeness crabs). Model results suggest strong effects of reduced

pH on nearshore state-managed invertebrate fisheries but modest effects on the

groundfish fishery. Our results provide a set of projections that generally support and

build upon previous findings and set the stage for hypotheses to guide future modeling

and experimental analysis on the effects of OA on marine ecosystems and fisheries.

51   **Introduction**

52   Humans rely on healthy ocean ecosystems for the benefits and services they provide.

53   However, global climate changes caused by continued fossil fuel emissions are subjecting

54   the oceans to multiple stressors (Harley *et al.*, 2006; Crain *et al.*, 2008; Solomon *et al.*,

55   2009). As oceans cover a majority of the Earth's surface and provide critical resources

56   for human communities, understanding how future climate conditions will affect factors

57   such as food security and coastal economies is a central question in climate change

58   research (Crain *et al.*, 2008). This question must be addressed at a global scale, but also

59   for downscaled bio-physical interactions within individual ecosystems (Barange *et al.*,

60   2014), expressed in terms of regional and national ecosystem services such as fisheries,

61   recreation, and coastal protection (Gattuso *et al.*, 2015).

62   Global change manifests in the ocean in multiple ways, one of which is ocean

63   acidification (OA), the process by which oceans absorb anthropogenic CO_2 from the

64   atmosphere and experience decreased pH and carbonate ion concentrations (Orr *et al.*,

65   2005; Doney *et al.*, 2009). Dissolution of CO_2 in water creates free hydrogen ions,

66   lowering the pH and thus altering a defining trait of the seawater to which marine

67   organisms are adapted. The oceans absorb about one-third of the anthropogenic CO_2

68   released into the atmosphere. Since the mid-1700s, this CO_2 uptake has decreased mean

69   pH in surface ocean waters by 0.1 units; by the end of this century, surface ocean pH may

70   decline by an additional 0.3 units (Caldeira & Wickett, 2003), with changes likely to vary

71   spatially (McElhany & Busch, 2013).

72   Upwelling systems may be particularly vulnerable to OA because they already

73   experience seasonal drops in pH compared to other ocean ecosystems (Feely *et al.*, 2008).

74   The upwelling process brings deep, cold, nutrient-rich waters up onto the continental

75   shelf, fueling highly productive coastal ecosystems. However, these upwelled waters also

76   have relatively low pH and low oxygen concentrations, and thus introduce potentially

77   stressful conditions into coastal areas. Alternatively, regular exposure to low pH could

78   lead to higher rates of adaptation to changing ocean chemistry (Reum *et al.*, 2014).

79   Regardless, changes to ocean chemistry have the potential to affect susceptible marine

80   organisms, particularly those that lay down a calcium carbonate shell (Kroeker *et al.*,

81   2013; Wittmann & Pörtner, 2013). Calcifiers include species such as bivalves,

82   crustaceans, and echinoderms that are commercially and ecologically important; as such,

83   the direct and indirect effects of OA may be widespread throughout a foodweb (Kaplan *et*

84   *al.*, 2010; Busch *et al.*, 2013).

85   Here, we focus on the California Current, an Eastern Boundary Current ecosystem where

86   the physical processes that combine upwelling with changing ocean chemistry have been

87   studied extensively (Feely *et al.*, 2008; Gruber *et al.*, 2012). Understanding cumulative

88   impacts of OA at the scale of an ecosystem like the California Current requires models

89   that can project direct and indirect effects. For example, end-to-end models (Plagányi,

90   2007; Travers *et al.*, 2007; Rose *et al.*, 2010) that incorporate processes like physics,

91   multi-species trophic effects, and fisheries can be used to simulate future projections of

92   ecosystem dynamics and to evaluate trade-offs among alternative fishery management

93   strategies (Fulton *et al.*, 2014), while evaluating consequences of global change (Lehodey

94   *et al.*, 2010), and coupling between oceanography and species dynamics (Fiechter *et al.*,

95   2014). Atlantis (Fulton, 2004; Fulton *et al.*, 2011) is a spatially explicit end-to-end model

96   that includes physical oceanography, biogeochemistry food web dynamics, and human

97   uses and impacts such as fishing and nutrient loading. The Atlantis framework has been

98   applied in simple ways to test impacts of ocean acidification in Australia (Griffith *et al.*,

99   2011, 2012) and Guam (Weijerman *et al.*, 2015). Atlantis models have been developed

100   for the California Current (Brand *et al.*, 2007; Horne *et al.*, 2010) and applied to test

101   impacts of new and existing fisheries (Kaplan *et al.*, 2013; Marshall *et al.*, 2014) and

102   alternative management strategies (Kaplan *et al.*, 2012; Pacific Fishery Management

103   Council & NMFS, 2014), as well as coarse scale effects of ocean acidification (Kaplan *et*

104   *al.*, 2010).

105   Building on these earlier Atlantis modeling efforts, we projected the cumulative effects of

106   future ocean acidification on the California Current ecosystem. First, we projected pH in

107   the California Current 50 years in the future (2063), using global earth systems models to

108   force a regional ocean-climate model (dynamical downscaling). This regional model

109   provided the physical conditions that underpinned Atlantis simulations of marine food

110   web interactions and US West Coast fisheries dynamics. We lowered survival of

111   functional groups sensitive to changing pH, based on a meta-analysis of experimental

112   studies. We then ran Atlantis scenarios that simulated: 1) the direct effects of a 0.2 unit

113   change in pH by 2063 on biomass of organisms sensitive to acidification; 2) the indirect

114   effects of changing pH on the rest of the food web; and 3) the resulting effects on

115   fisheries landings and revenues.

116   **Methods**

117   Atlantis is a spatially explicit modeling platform (Fulton, 2004) that couples three sub-

118   models: 1) an oceanographic sub-model, 2) an ecology sub-model, and 3) a human sub-

119   model (Figure 1). We focused on the first two components for this application and used a

120   simple representation of fishing for the third component. Below we summarize the three

121   sub-models, how we parameterized pH sensitivity, and the scenarios we developed to

122   investigate the effects of changing pH on the California Current ecosystem. Our current

123   application of the California Current Atlantis model builds on and updates earlier

124   versions (Brand *et al.*, 2007; Horne *et al.*, 2010; Kaplan *et al.*, 2012). Additional details

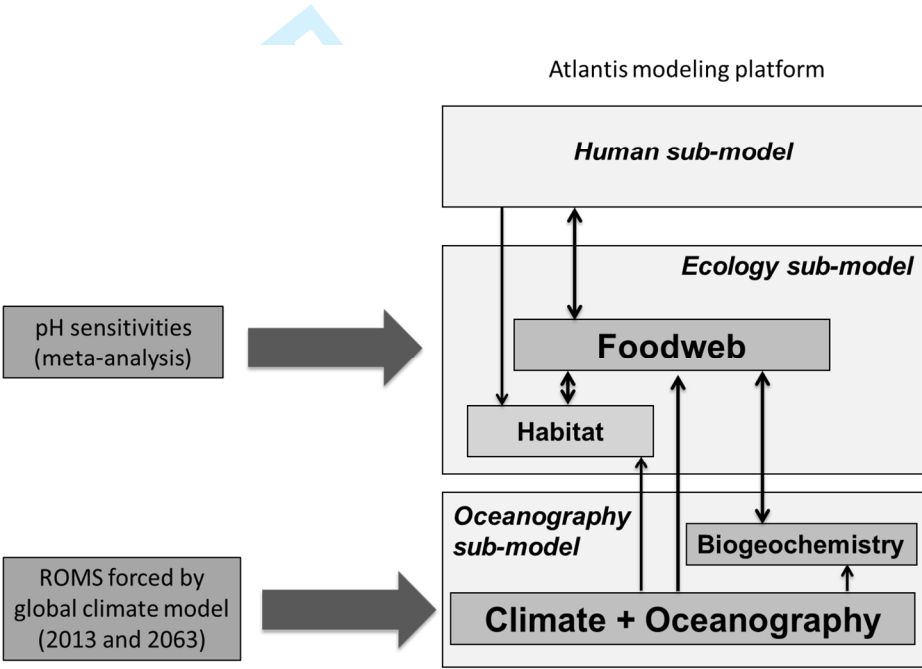125   are available in the online Supplementary Materials.

126
127
128   **Figure 1.** Conceptual diagram of modeling approach for the California Current Atlantis
129   Model. The general diagram of the Atlantis platform and the three coupled sub-models
130   are shown on the right, with the key modifications and points of entry for information
131   related to this application for projecting ocean acidification shown on the left.
132

133   *Model domain*

134   Our model domain covers 1.475 million km^2, with 92,000 km^2 on the continental shelf

135   (0-200 m), 127,500 km^2 on the continental slope (200-1200 m), and 1.12 million km^2 in

136   pelagic waters offshore of the 1200-m isobath. The model domain covers the extent of

137   the California Current, from its origin where the North Pacific Current meets the coast of

6

138   North America at the north end of Vancouver Island (Checkley & Barth, 2009) south to

139   Punta Eugenia, Baja California, Mexico (Figure 2). The domain is divided into 2-

140   dimensional polygons. Longitudinal breaks follow the bathymetry of the 50-m, 100-m,

141   200-m, 550-m, and 1200-m isobaths, and the 200-nautical mile (370-km) limit of the

142   Exclusive Economic Zone (EEZ). Latitudinal breaks were based on a compromise

143   between biogeography, fishery management and catch reporting areas, and areas utilized

144   by particular fleets and fisheries. Three-dimensional model cells are created by adding

145   depth layers in vertical dimension, which were set using the same interval as isobaths

146   listed above. The offshore pelagic polygons, which extend from the 1200-m isobath to

147   the EEZ limit, are assumed to be 2400 m deep (with an open boundary representing

148   deeper waters lying underneath and along the western boundary of this upper ocean slab).

149   We refer readers to the online Supplementary Materials for further description and

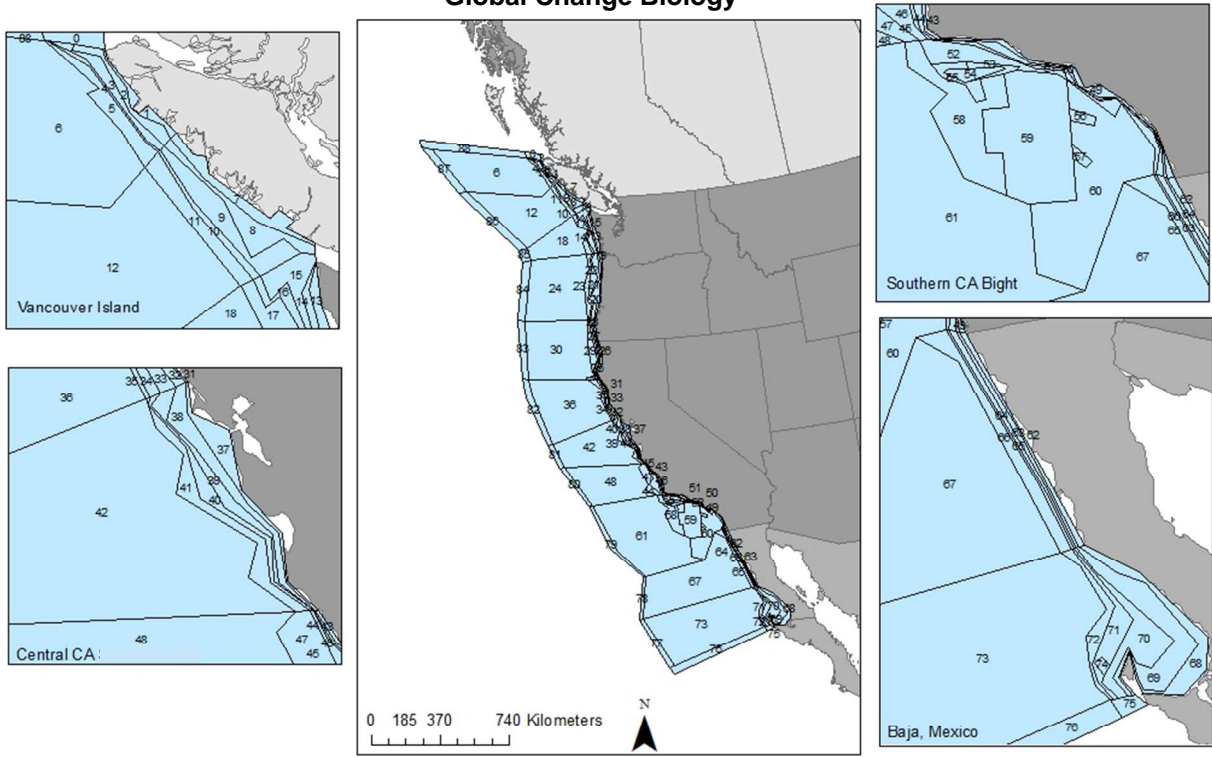150   justification of the model domain.

151   **Figure 2.** Map of California Current Atlantis model domain
152

153   *Oceanographic Sub-model: Regional Ocean Modeling System (ROMS)*

154   To capture the local effects of global change between years 2011-2020 and 2061-2070,

155   we coupled a high resolution Regional Ocean Modeling System (ROMS, version 3.7,

156   (Moore *et al.*, 2011)) to global circulation models and Intergovernmental Panel on

157   Climate Change (IPCC) CO_2 scenarios. The results capture effects of global change on

158   pH, temperature, nutrients, and oxygen on an ecologically relevant spatial scale. We

159   discuss this briefly below, and in detail in the Supplementary Materials (Appendix A).

160   To represent global climate, we used output from the GFDL ESM2M earth system model

161   (Dunne *et al.*, 2012, 2013) driven under IPCC climate scenario RCP8.5, which assumes

162   continuation of present emissions trajectories (Moss *et al.*, 2010). ESM2M includes an

163   embedded global biogeochemical/NPZ model (TOPAZ, Stock *et al.*, 2014). We used

164   ESM2M results to generate the initial and boundary conditions for ROMS. ROMS is

165   well-suited to resolve small-scale coastal phenomena, and has been successfully applied

166   in a wide range of regional studies worldwide (Haidvogel *et al.*, 2008). The ROMS

167   spatial domain was chosen to encompass the domain of the Atlantis model with ~10-km

168   grid spacing. We included tidal forcing, and applied atmospheric forcing from the

169   ESM2M projections using bulk formulae (Fairall *et al.*, 1996, 2003). We used a regional

170   nutrient-phytoplankton-zooplankton (NPZ) model coupled within the ROMS code, which

171   is based on that of Fennel et al. (Fennel *et al.*, 2006, 2008) and includes carbonate

172   dynamics. Initial and boundary conditions for the NPZ variables were supplied from the

173   global TOPAZ output. The primary output of this coupled ESM2M-ROMS system is a 3-

174   dimensional gridded field of time series of temperature, salinity, water flux (currents),

175   and pH (derived from the carbonate output) in the California Current. We interpolated

176   these four variables onto the Atlantis spatial domain, and forced their values within the

177   Atlantis simulations described below. We note that future climate scenarios did not

178   include changes to primary productivity due to increased atmospheric carbon dioxide.

179   *Ecology Sub-model*

180   Our ecology sub-model represents the food web of the California Current, simulating

181   population dynamics, movement, and ecological interactions of 75 different functional

182   groups. The functional groups, data sources, and core biological and ecological

183   parameters and functional forms are detailed in Appendix A. Generally, functional

184   groups are aggregates of species with similar life histories, habitats, and diets, with finer

185   taxonomic resolution for harvested fish or species of conservation concern, and coarser

186   aggregation of many invertebrate groups. This model updates and improves on data

187   sources used in an earlier version of the California Current Atlantis model (Horne *et al.*,

188   2010), and functional groups were added to allow for better representation of processes

189   related to ocean acidification. In particular, groups added or given finer taxonomic

190   resolution in the present model were three coral taxa (stony corals, soft corals, and black

191   corals), Dungeness crab (*Metacarcinus magister*), pteropods, coccolithophores, and

192   market squid (*Doryteuthis opalescens*). In total the model includes 25 benthic and

193   planktonic invertebrate groups, five primary producer groups, 36 fish groups, 10 marine

194   mammal groups, two bird groups, and two detritus groups. Invertebrates and primary

195   producers are represented as simple dynamic biomass pools per 3-dimensional model

196   cell, while vertebrate age and size structure are modeled explicitly and vary through time.

197   Results below are presented both as functional groups and also in simplified, aggregated

198   guilds such as 'Sharks' or 'Demersal Fish'.

199   Recruitment of vertebrates (the production of juveniles) is based on the total abundance

200   of adults, and recruits in the model are distributed spatially proportional to adult

201   abundance. Recruitment of fish follows Beverton-Holt stock-recruitment dynamics

202   (Beverton & Holt, 2012). When stock assessments were available, initial parameter

203   estimates for Beverton-Holt parameters were calculated based on estimates of steepness

204   (slope of the stock-recruit curve at the origin), unfished recruitment, and unfished

205   spawning biomass. Recruitment of marine mammals, sharks, and birds were based on

206   estimates of a fixed number of offspring per adult per year.

207   To parameterize diets, we drew from the database compiled by Dufault et al. (2009),

208   which we updated to reflect the new functional group structure of the model and also to

209   incorporate new literature sources, including many contributed by Szoboszlai et al.

210   (2015). Those additions are noted in the Supplementary Materials (Appendix A).

211   *Human sub-model: Fishing mortality*

212   As noted above, the representation of human activities (other than anthropogenic-driven

213   climate change) in these simulations is restricted to fishing, and this representation is

214   quite simple. We assembled catch information for all Atlantis functional groups,

215   summing total catches across US, Canada, and Mexico (Appendix A)**.** We did not model

216   specific fleets, but instead implemented a fixed fishing mortality rate (yr^{-1}). This fishing

217   mortality gives a catch for the initial year of the simulation (2013) equal to summed 2013

218   US, Canadian, and Mexican catches. Fishing mortality rates were distributed evenly in

219   space and we did not include marine protected areas or other forms of spatial

220   management. Because fishing removes a fixed proportion of a species in each year,

221   catches are proportional to biomass throughout these simple simulations.

222   *Parameterizing pH sensitivity and response to changing pH*

223   Our scenarios for pH impacts on invertebrate survival derive from a study by Busch and

224   McElhany (submitted), which synthesized 393 papers reporting temperate species

225   sensitivity to changes in seawater carbon chemistry. In that manuscript, summary

226   understanding of the relative sensitivity of functional groups in the California Current

227   ecosystem was based on how well published studies related to functional groups in and

228   pH conditions of the California Current ecosystem, experimental design and quality, and

229   the type of variables measured to characterize sensitivity. The results of Busch and

230   McElhany (submitted) focus on a qualitative ranking of the sensitivity of survival of

231   California Current functional groups to declines in pH, and they translate this qualitative

232   ranking into a scalar that describes the relationships between functional group survival

233   and pH (Table 1). We focused on species that showed the strongest direct negative effects

11

234   of pH on survival (primarily calcifiers).   This is consistent with previous global efforts to

235   synthesize effects of acidification, namely strong negative impacts on calcifiers such as

236   corals and mollusks, but a broader range of detectable impacts on other invertebrates

237   (Kroeker et al., 2013, 2010; Wittmann and Pörtner, 2013).

238   **Table 1**. Scenario descriptions for projections of the effects of ocean acidification on the
239   California Current ecosystem. Affected functional groups are listed by Scenario with
240   their relative survival scalar that indicates that groups sensitivity to declines in pH (as per
241   Busch and McElhany (submitted)).

Scenario	Affected Functional Groups	Relative Survival Scalar	Example species
Calcifiying Benthos	benthic herbivorous grazers	-1	sea urchins (*Allocentrotus fragilis*), snails
	bivalves	-0.89	bivalves
	shallow benthic filter feeders	-0.55	tunicates, sponges
Copepods & Pteropods	mesozooplankton	-0.99	copepods
	pteropods	-0.81	thecosome pteropods
Crabs & Shrimp			crabs (excluding Dungeness crab)
	crabs	-0.7	
	crangon shrimp	-0.45	shrimps (excluding pandalids)
	Dungeness crab	-0.41	Dungeness crab
Non-calcifying Benthos	carnivorous infauna	-0.39	polychaetes, nematodes
	deposit feeders	-0.37	amphipods, isopods

242
243   The survival scalars in Busch and McElhany (submitted) represent our best

244   understanding of acidification impacts in the California Current. We translated their

245   values into effects on mortality that we implemented in the Atlantis model. Specifically,

246   we defined mortality due to pH effects for each functional group *f* in Atlantis polygon *p*

247   at time-step *t* as:

248   *(1)* $M_{fpt}^{pH} = (8.0 - pH_{pt}) \times S_f$

249   where M_{fpt}^{pH} is in units of yr $^{-1}$, pH is specified by Atlantis spatial polygon and time-step,

250   and S_f is -0.1* the relative survival scalar for each functional group (Table 1). A pH of

251   8.0 was chosen because average pH in the top 200 m of the water column for ROMS year

252   2013 was ~7.95. If pH_{pt} was greater than 8.0, M_{fpt}^{pH} was set to zero. As an example, this

253   parameterization implies that for the most sensitive functional group (Benthic

254   Herbivorous Grazers, containing species such as non-nearshore sea urchins), a decrease

255   in pH from 8.0 to 7.0 increased their mortality rate by 0.1 yr^{-1}. We also tested alternate,

256   stronger assumptions about mortality due to pH, increasing S_f by up to tenfold (described

257   below).

258

259   *Ocean Acidification Scenarios*

260   We simulated direct effects of acidification on the ten functional groups with the

261   strongest negative ocean acidification responses, based on Busch and McElhany

262   (submitted). We grouped these ten functional groups into four scenarios: Benthic

263   Calcifiers, Non-Calcifying Benthos, Copepods and Pteropods, and Crabs and Shrimps

264   (Table 1). For each scenario, we tested the effects of 2063 pH and oceanographic

265   conditions and pH sensitivity on the functional groups within that scenario. We also

266   tested an additional scenario where all groups in Table 1 were simultaneously sensitive to

267   pH (referred to as the "Cumulative" scenario below).

268   All scenarios ran for 100 simulated years, with initial biological conditions set to year

269   2013, and constant fishing mortality at 2013 rates (units of yr^{-1}), but with the ROMS

270   oceanography (including pH) for a single year looped 100 times. We ran two baseline

271   simulations with no OA sensitivity, one using 2013 ROMS oceanography and one using

13

272   2063 ROMS oceanography. Runs with OA sensitivity used 2063 ROMS oceanography.

273   We used a single year of ROMS oceanography for two reasons: 1) creating a 50 year

274   downscaled hydrodynamic model was too computationally intensive, and 2) using a

275   single year of ROMS oceanography controlled for interannual variability in ocean

276   conditions and allowed us to isolate the effects of ocean acidification from other potential

277   drivers of change. We note that 2063 ROMS oceanography included increases in

278   temperature as well as decreased pH, and we isolated the effects of changing pH using

279   the baseline runs (see *Metrics of pH effects* below).

280   To test model sensitivity to our quantitative interpretation of the rankings from Busch and

281   McElhany (submitted), we repeated all 5 scenarios but with 2.5, 5, and 10x stronger

282   increases in mortality per 1 unit decline in pH. The most extreme case (10x) would

283   increase mortality rates for Benthic Herbivorous Grazers by 1.0 yr^{-1} if pH fell from 8.0 to

284   7.0, and proportionally smaller mortality increases among the other groups, based on the

285   Relative Survival Scalars (Table 1).

286

287   *Metric of pH effect*

288   Recognizing that multiple factors in the physical environment change when projecting

289   future oceanography, we wanted to isolate the effects of changing pH. We developed a

290   metric that standardizes the pH sensitivity of functional groups within a scenario (Table

291   1) while accounting for changes in circulation and other food web effects. The relative

292   effect (*E*) of changing pH on biomass (*B*) for each functional group is:

293   *(2)* $$E = \frac{B_{test} - B_{2063Baseline}}{B_{2013Baseline}}$$

14

294   where B_{test} is the biomass of a group in a given scenario, $B_{2063Baseline}$ is the biomass for the

295   group in the baseline model with future circulation, and $B_{2013Baseline}$ is the biomass for the

296   group in the baseline model with present circulation. For each simulation, we used the

297   mean biomass of the final 10 years of a 100-year run for B. While it is difficult to

298   determine what constitutes a non-zero effect, we follow the conventions of similar

299   ecosystem modeling exercises (Smith *et al.*, 2011; Kaplan *et al.*, 2013; Marshall *et al.*,

300   2014), focusing on $|E| > 0.20$. Focusing on these large effects is consistent with the

301   overall strategic rather than tactical use of this type of end-to-end model (FAO, 2008) and

302   means that attention is on effects of a magnitude likely to be readily detectable should

303   they occur in real world observational data.

304   *pH effects on fishery revenue*

305   We translated the effects of pH on biomass (*E in Eq. 2*) to revenue using 2013 landings

306   and revenue data (PacFIN 2013). Because fishing mortality was fixed at 2013 rates in

307   our simulations, the effect of pH on fisheries catches is equivalent to the pH effect on

308   biomass. We grouped functional groups into coarser management units and projected the

309   effects of changing pH on revenue at that scale. Within the US fishery management

310   system, individual species (and therefore Atlantis functional groups) fall within distinct

311   management units, governed by one of several federal Fishery Management Plans

312   (FMPs) or by state plans (deReynier, 2014). We show results for the following units:

313   State (including all crabs and shrimps, nearshore urchins, bivalves), Groundfish (all

314   commercially landed groundfish except Pacific Hake), Pacific Hake, and Coastal Pelagic

315   Fish (sardine, anchovy, mackerels). We calculated the pH effect on revenue (*U*) for each

15

316   management unit k as a weighted average of its component functional group effects ($\underline{E_j}$)

317   such that:

$$U_k = \frac{\sum E_j * R_{j\ 2013}}{\sum R_{j\ 2013}}$$

318   Where the weight R_j is the 2013 revenue for functional group j, and revenue was

319   calculated as the product of U.S. price per metric ton and expected 2013 catch for each

320   functional group. Additional details on reconstructing 2013 catch are provided in the

321   Supplementary Online Material (Appendix A).

322   *Calibrating the ecology sub-model*

323   Following guidelines developed for an earlier version of the California Current Atlantis

324   model (Horne *et al.*, 2010), we calibrated the model in two phases: initial simulations

325   with no fishing; and secondary calibrations testing constant fishing pressure. Atlantis

326   explicitly models numbers-at-age (or number-per-cohort), and dynamic weight-at-age,

327   and we evaluated these emergent properties following a Pattern Oriented Modeling

328   approach (Grimm *et al.*, 2005). Secondary calibration tested a range of fixed levels of

329   fishing mortality applied simultaneously to all groups. As a rule of thumb we expected

330   that F_{MSY} might fall within 0.5-0.8 of natural mortality rates (Patterson, 1992; Patterson *et*

331   *al.*, 2001; Walters & Martell, 2002).

332

333   **Results**

334   *ROMS forced with ESM2M*

16

335   Our ROMS projection of future ocean conditions (year 2063) suggests marked declines in

336   pH relative to present day simulations (year 2013). In the top 100 m of the water column,

337   mean August pH in the ROMS model declines from 7.96 in the present day to 7.77 in the

338   future (Figure 3); this is equal to the ~0.2 unit drop in pH predicted by the coarser

339   ESM2M model (Appendix A, Figure A2), and represents a 55% increase in acidity (e.g.,

340   55% change in $[H^+]$). As expected, the late summer period depicted in Figure 3 has the

341   lowest pH of the year, in response to the preceding spring-summer upwelling period that

342   characterizes the California Current. ROMS effectively represents the present day spatial

343   pattern we expect for the system as well, with summertime reductions in pH along the

344   coast, and a shoaling of pH clines near shore (Appendix A, Figures A3, A4). Compared

345   to ESM2M, the spatially downscaled ROMS yields much finer predictions of spatial

346   patchiness of future acidification; for example, some of the lowest pH values are

347   predicted to occur very close to shore at depth (Figure 3d), and the northern continental

348   shelf is predicted to experience slightly greater pH than in regions south of 40°N latitude

349   (Figure 3c, d). This spatial resolution is critical for driving the future pH responses of

350   biological groups within each Atlantis polygon. In addition, ROMS predicts warmer

351   conditions in 2063 relative to 2013; the annual mean temperature increase in the upper

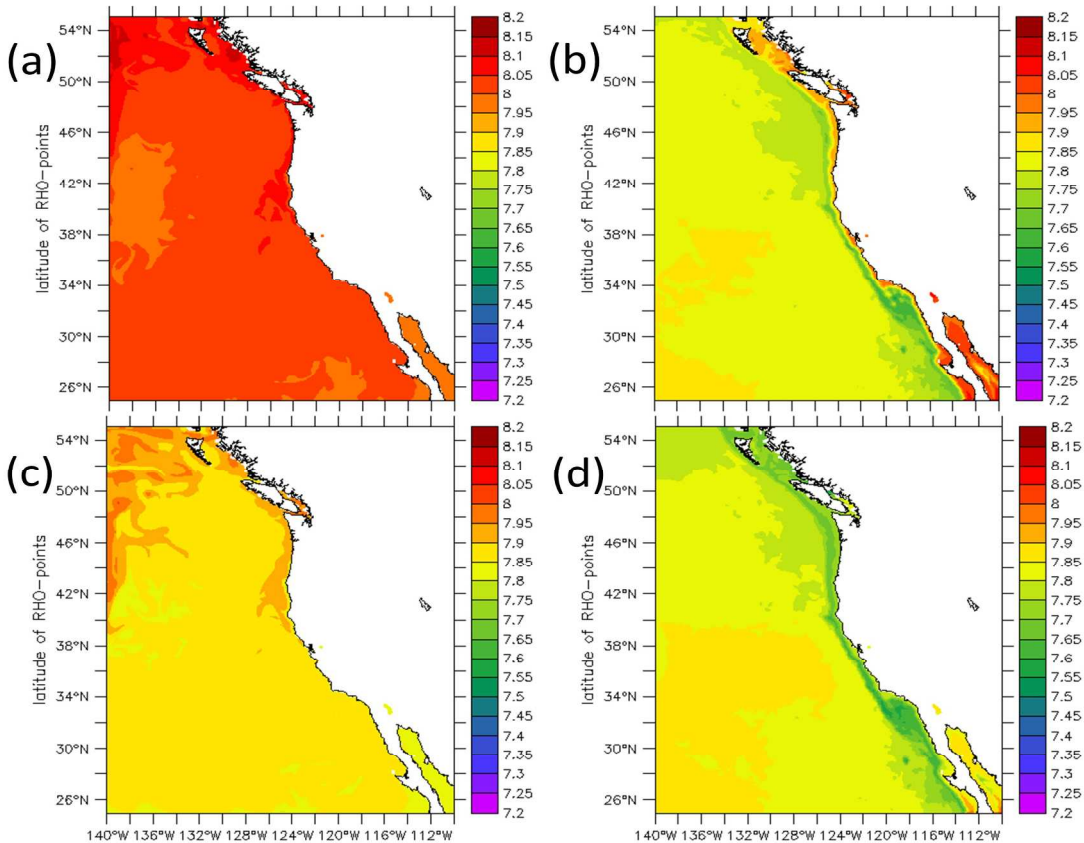352   100 m of the water column is 0.9°C.

Figure 3. ROMS projections of pH in August 2013 (a and b) and August 2063 (c and d), at the surface (a and c) and bottom (b and d). ROMS runs are initialized Jan 1, 2010 or Jan 1, 2060, and are forced by GFDL ESM2M under IPCC RCP 8.5. pH within ROMS is calculated from carbonate variables simulated using the model of Fennel et al. (2006, 2008).

Calibrating and validating the ecology sub-model

Initial simulations with no fishing resulted in 86% of functional groups persisting for

more than 50 years (Appendix A, Tables A1 and A2), with quasi-stable population

dynamics for most groups after approximately year 50. Similar to other simulation

modeling efforts (Gaichas *et al.*, 2012; Thorpe *et al.*, 2015), we found that ensuring

persistence of all functional groups was not trivial, and we were forced to accept a

parameterization that allowed 11 functional groups to decline to low levels in base case

simulations (without ocean acidification). These functional groups were excluded from

the analysis: arrowtooth flounder, pelagic sharks, sea stars and brittle stars, pandalid

18

368   shrimp, grenadiers, large phytoplankton, market squid, Pacific Ocean perch, large pelagic

369   predators, Chinook salmon, and large demersal predators.   The excluded species

370   comprise <2% of vertebrate biomass and ~1% of heterotroph (consumer) biomass. The

371   excluded species represent 28% of the revenue generated in 2013, and do not include the

372   top two fished species by 2013 landings (Pacific sardine and Pacific Hake). For persisting

373   species, we obtained sensible age structures and weight-at-age within tolerance; e.g.,

374   within ±50% of initial values and ideally within ±20% (Horne *et al.*, 2010).

375   Secondary calibration suggested fishing rates at maximum sustainable yields (F_{MSY}) near

376   0.05-0.1 for most groundfish stocks, with higher values (>0.2) for most pelagic species

377   (Appendix B). This was consistent with expectations that demersal stocks have lower

378   productivity, as evidenced by lower estimates of natural mortality (Appendix B). We also

379   found that most groups targeted by commercial fishing were able to sustain fishing

380   mortality held at 2013 levels. Two functional groups, petrale sole and shallow small

381   rockfish, persisted in unfished simulations and were included in our analyses of outputs,

382   but showed strong biomass declines under relatively moderate fishing (see Appendix B).

383   Therefore, interpretation of results regarding these groups should be cautious.

384   *Effects of future pH on biomass*

385   Applying 2063 pH projections within 100-year Atlantis simulations caused a wide range
386   of effects across the ecosystem, and most of these effects were negative (Figure 4). In
387   general, there were few strong guild-level responses to decreasing pH (Figure 4A). Only
388   one guild-level pH effect was stronger than the $|E| > 0.2$ threshold (Epibenthos in the
389   Calcifying Benthos scenario). Overall, the functional groups in the Demersal Fish and
390   Epibenthos guilds exhibited the highest variability, with some groups experiencing a
391   strong pH effect and others little to no effect. Several guilds (Mammals, Seabirds, Pelagic
392   Fish, Squid, and Primary Producers) were insensitive ($|E| < 0.2$ for all functional groups)
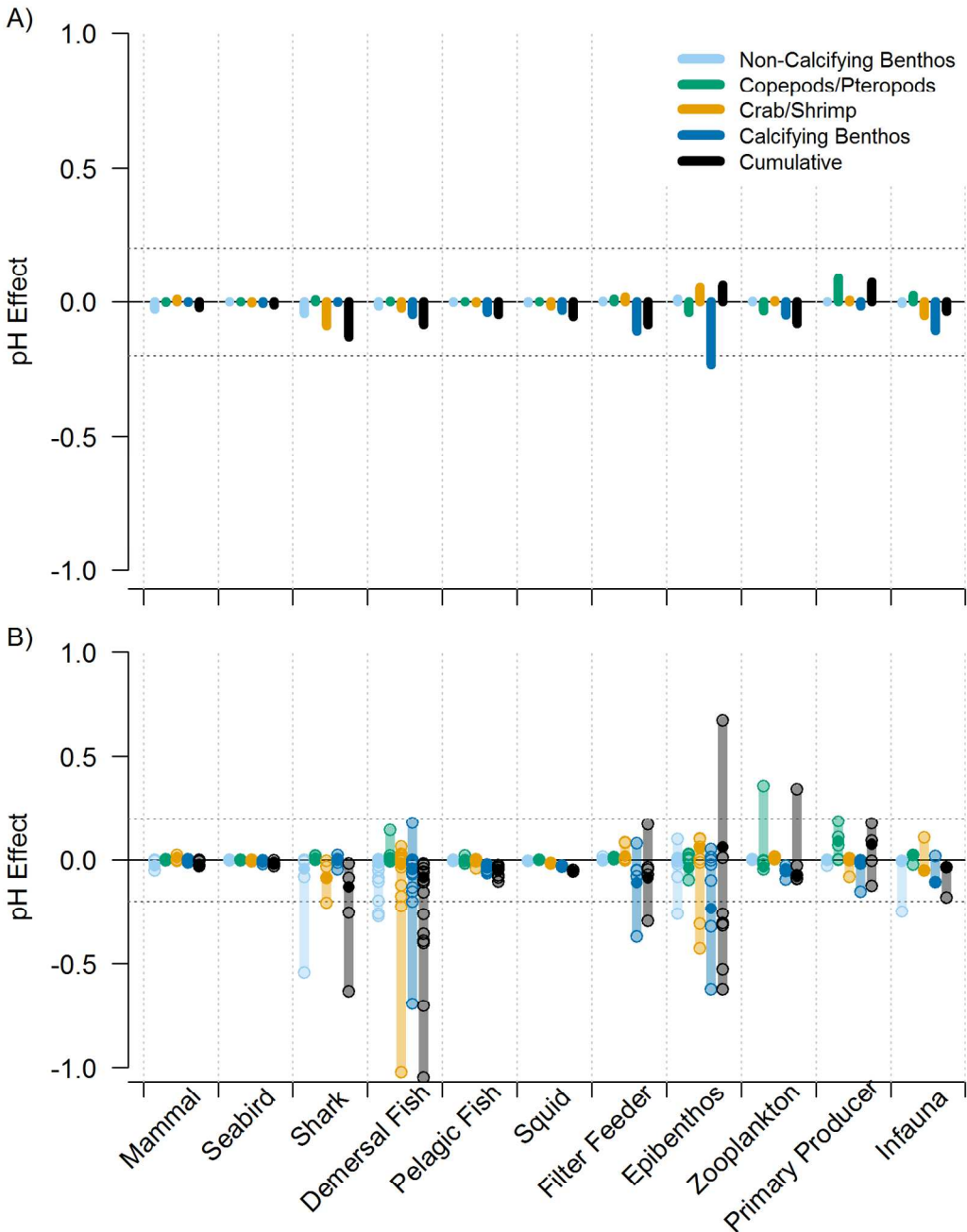393   across all the scenarios.

Figure 4. Ecosystem responses to forecasted pH for guilds in the California Current Atlantis model. We ran five OA scenarios, varying the sensitivity of Non-calcifying benthos (light blue), Copepods and Pteropods (green), Crabs and Shrimp (yellow), Calcifying Benthos (dark blue), and a Cumulative scenario with all of the previous scenarios combined (black). Biomass-weighted mean pH effect (E) shown as the heights of the bars in (A) and individual functional group responses in (B). Solid circles in B indicate the mean guild-level effect shown in A for comparability. Horizontal dotted lines at E=±0.2 indicate the threshold that we considered a strong effect.

404   In contrast to the few guild-level effects of changing pH, many individual functional

405   groups responded strongly in each scenario (Figure 5). The scenarios directed at

406   Calcifying Benthos, Non-Calcifying Benthos, and Crabs and Shrimps each had five

407   functional groups with $|E| > 0.2$. In contrast, only one functional group

408   (microzooplankton) responded strongly to the scenario directed at Copepods and

409   Pteropods. The Cumulative scenario, which applied future conditions and pH sensitivity

410   to all 10 functional groups in Table 1, led to strong responses in 16 functional groups

411   (Figure 5).

412
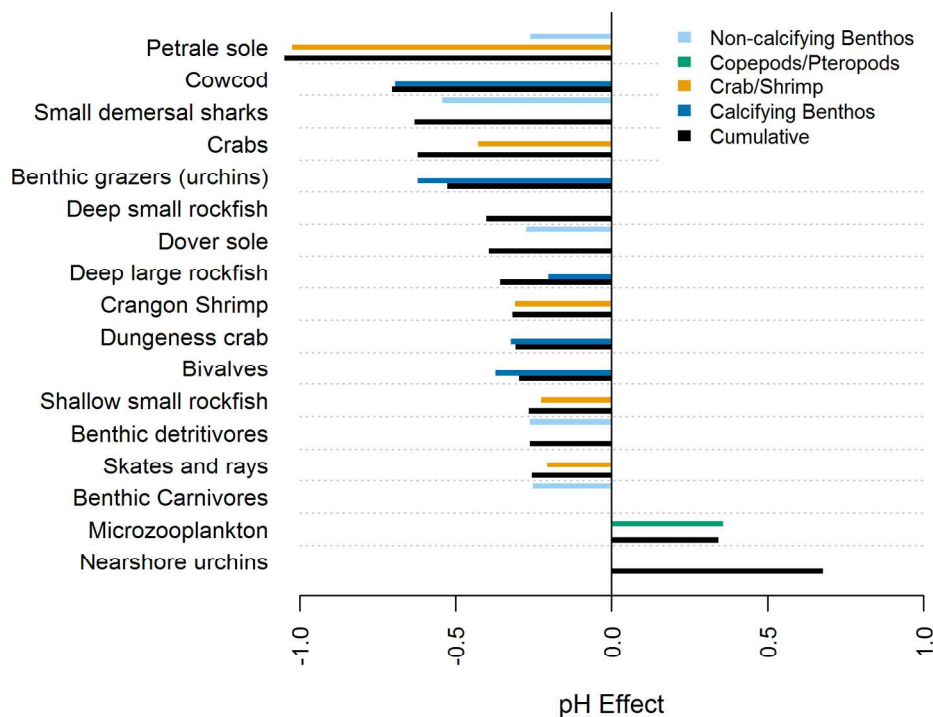413   **Figure 5.** Projected effects of future pH on functional group biomass for those groups
414   with a strong effect ($|E| > 0.2$). Bars are colored according to scenario, with the same
415   colors as in Figure 4 (Non-calcifying benthos (light blue), Copepods and Pteropods
416   (green), Crab and Shrimp (yellow), Calcifying benthos (dark blue), and Cumulative
417   (black)).
418

21

419   Sensitivity to pH in the Calcifying Benthos scenario led to strong direct effects of future

420   pH on benthic grazers and bivalves, but no direct effects on shallow benthic filter feeders

421   (Figure 5). Declines in benthic grazers and bivalves led to declines for three of their

422   predators: cowcod, deep large rockfish, and Dungeness crab. All negative effects

423   observed in Calcifying Benthos scenario were retained when pH sensitivity was added to

424   other groups in the Cumulative scenario.

425   Applying pH sensitivity and future climate conditions in the Crabs and Shrimps scenario

426   resulted in strong direct effects on the general crab group and crangon shrimp, but not

427   Dungeness crab (Figure 5). Strongly negative indirect effects occurred on petrale sole,

428   shallow small rockfish, and skates and rays, all of which depend heavily on crangon

429   shrimp in their model diets. All of the negative effects observed in the Crabs and Shrimp

430   scenario were also present in the Cumulative scenario, and strong negative effects on

431   Dungeness crab emerged in the Cumulative scenario.

432   The Non-Calcifying Benthos scenario resulted in strong direct negative effects in both

433   sensitive functional groups: benthic detritivores and benthic carnivores (Figure 5). Petrale

434   sole, small demersal sharks, and Dover sole experienced strong indirect negative effects

435   in this scenario even though none of these species preys directly on the pH-sensitive

436   groups. It is likely these indirect effects were modulated through a shared prey group

437   (e.g., crangon shrimp) that was weakly affected by declines in benthic detritivores and

438   benthic carnivores. All negative effects in the Non-Calcifying Benthos scenario were also

439   present in the Cumulative scenario, except benthic carnivores were only weakly affected

440   ($E < |0.2|$) when all species were sensitive to pH.

22

441   The Copepods and Pteropods scenario resulted in no strong responses by either of the

442   directly affected groups: Copepods and pteropods declined by 2 and 5 %, respectively.

443   However, copepods are a very abundant group (estimated at nearly 20 million metric tons

444   for our large model domain; Appendix A, Table A1), and this is a substantial shift in

445   absolute terms. Microzooplankton, a prey group for both copepods and pteropods,

446   responded strongly in the positive direction to the negative effects on its predators

447   (Figure 5). This indirect effect was also seen in the Cumulative scenario.

448   The Cumulative scenario produced more strong responses than the preceding scenarios,

449   primarily negative responses by Demersal Fishes and Epibenthos (Figure 4). It also

450   resulted in two strong indirect effects not observed in any of the other scenarios (Figure

451   5). Deep small rockfish, which prey upon many of the pH-sensitive groups, responded

452   negatively ($E = -0.40$) when all of the sensitive groups declined with pH. The other new

453   indirect response was by nearshore urchins, which had a strong positive response ($E =$

454   0.68). Nearshore urchins are fed upon by many of the fish groups that experienced

455   indirect negative effects. Moreover, nearshore urchins were assumed not to be directly

456   sensitive to ocean acidification; the meta-analysis of Busch and McElhany (submitted)

457   suggests that these commercially harvested nearshore urchins are less susceptible to

458   acidification than our benthic herbivorous grazers group, which includes deeper-dwelling

459   urchin species.

460   *Effects of future pH on catch and revenue in Cumulative scenario*

461   Our simplistic representation of fishing and revenue projected that most fishery

462   management units we explored were negatively affected by future pH in the Cumulative

463   scenario (Table 2). Proportional effects of pH on catch and biomass at the functional

464 group level are equal because we parameterized fishing using fixed fishing mortality rates

465 for each functional group. The State-managed unit had the largest projected pH effect on

466 revenue (U = -0.29), driven by the strong negative effect of pH on Dungeness crab, which

467 supports a valuable fishery (200 million USD in 2013). Other crabs and bivalves were

468 negatively affected by future pH, but the 2013 revenue from those fisheries is an order of

469 magnitude lower than the Dungeness crab fishery. The urchin fishery targets the

470 nearshore urchin group, which was the only harvested functional group that was

471 projected to increase under future pH conditions.

472 **Table 2.** Effects of future pH on commercially important management units, from the
473 scenario with all groups in Table 1 sensitive to pH. Management units are listed in order
474 of greatest to least effects of pH on revenue, and the three-four most strongly affected
475 functional groups within those management units are identified.
476

Management Unit	Most Affected Functional Groups	pH Effect Biomass and Catch	pH Effect Revenue	Baseline Revenue (millions USD)
State			-0.29	260
	Dungeness crab	-0.30		220
	crabs	-0.61		9.5
	bivalves	-0.29		17
	urchins	0.61		6.8
Groundfish			-0.18	88
	petrale sole	-1.1		7.5
	Dover sole	-0.39		9.0
	deep large rockfish	-0.35		5.0
Hake	hake	-0.038	-0.038	76
Coastal Pelagics			-0.0080	110
	sardine	-0.030		27
	jack mackerel	-0.050		1.5
	anchovy	-0.026		1.3

477

478   The Groundfish management unit (excluding Pacific hake) did not experience a

479   substantial pH effect on revenue (U=-0.18). This group of species generated $88 million

480   in revenue in 2013. While this decline was not dramatic ($|U| < 0.20$) for the total revenue

481   from species managed under the groundfish FMP, our model projects more substantial

482   declines for particular commercially important groundfish such as petrale sole, Dover

483   sole, and deep large rockfish (mostly shortspine thornyhead, *Sebastolobus alascanus*).

484   The remaining management units did not show strong effects of changing pH ($|U| < 0.2$).

485   The model projected a very small pH effect (U= -0.038) on Hake fishery revenue, in a

486   fishery generating 76 million USD of revenue in 2013. For species managed collectively

487   under the Coastal Pelagic Species FMP, the pH effect was less than 0.01. We do not

488   show results for Salmon or Highly Migratory Species FMPs due to the poor performance

489   of those species in the model (Chinook and large pelagic predators were removed due to

490   low biomass in baseline runs).

491   *Sensitivity of pH effects to strength of the pH response*

492   As would be expected a *priori*, the effects of future pH at the guild-level were sensitive to

493   the magnitude of the mortality scalar. The magnitude of positive and negative effects

494   increased as the scalar increased to 2.5x to 10x our base case values (Appendix C).

495   However, the directions of pH effects at the guild and functional group levels were

496   consistent regardless of the mortality scalar, as was the set of functional groups and

497   guilds identified as likely impacted by pH effects.

498   **Discussion**

499   *Interpretation of Atlantis results*

500   Global change is projected to have pronounced impacts on marine ecosystems and

501   resources in temperate zones. The climate change scenario applied here, IPCC scenario

502   RCP 8.5, will have high impacts on mid-latitude bivalve fisheries and aquaculture, and

503   high to moderate impacts on mid-latitude finfish fisheries, according to a growing body

504   of research (Barange *et al.*, 2014; Gattuso *et al.*, 2015). In fact, many symptoms of global

505   change are already being observed in the California Current ecosystem, including

506   warming, shifts in community structure and phenology (Thorson *et al.*, 2016), and major

507   hypoxic events (reviewed in Doney *et al.*, 2012). There is already evidence of ocean

508   acidification impacts: episodic year-class failures of Pacific oysters (*Crassostrea gigas*)

509   along the US West Coast have been attributed to OA (Barton *et al.*, 2012), and Bednaršek

510   and Ohman (2015) have documented OA-driven shell dissolution in the pteropod

511   *Limacina helicina* in the southern California Current.

512   Our modeling effort, which synthesized downscaled climate models, experimental and

513   empirical studies, and a well-established end-to-end marine ecosystem modeling

514   framework, provides a broad overview of potential ecosystem-scale effects of OA in the

515   California Current. We saw wide-ranging effects across multiple guilds and functional

516   groups, but more losers than winners in terms of biomass and lost fishery revenue. Model

517   predictions suggest the most dramatic effects of future pH decreases will be felt by

518   demersal fish, sharks, and epibenthic invertebrates, and less so by pelagic species, marine

519   mammals and seabirds. This was likely driven by the stronger responses of sensitive

520   benthic organisms to changing pH, compared to relatively weak responses of sensitive

521   zooplankton groups. Our approach demonstrated that combining multiple scenarios into a

522   single, cumulative scenario can lead to unanticipated, indirect responses by groups that

523   were relatively insensitive in simpler scenarios.

524   The value of taking both a population and systems approach is further evident when

525   comparing our preliminary ranking of direct pH responses (Table 1) to the cumulative

526   impacts projected by the Atlantis model (Figure 4 and 5). Although experimental and

527   empirical literature suggests that copepods, shallow benthic filter feeders, and Dungeness

528   crabs may be susceptible to OA (Busch and McElhany, submitted), none of them

529   responded strongly in scenarios where they were directly affected by pH. All three

530   functional groups exhibited relatively high productivity, which prevented substantial

531   declines in their biomass due to direct effects. Indirect effects were responsible for

532   declines in Dungeness crab, a major fishery target. We only observed a strong pH effect

533   on Dungeness crab when their prey declined due to OA (Calcifying Benthos scenario),

534   but not due to direct pH-driven mortality (Crabs and Shrimp scenario). This insight

535   highlights the utility of end-to-end models for comparing multiple scenarios (Busch *et al.*,

536   2013), as well as the ability of the Atlantis model to integrate over direct effects, indirect

537   trophic effects, and population-level productivity.

538   From a fishery management perspective, economic impacts in the California Current may

539   stem from indirect ocean acidification effects on high-value target species such as

540   Dungeness crab and groundfish. Previous research has focused on global economic and

541   nutritional losses due to projected direct ocean acidification effects on shellfish (Cooley

542   *et al.*, 2012), but our work suggests careful consideration must also be given to the

543   supporting role that shellfish and other species play in the food web. At a minimum,

544 economic impact assessments should include fisheries that target species dependent on

545 calcifying prey (e.g., Cooley & Doney, 2009).

546 Other investigations of future change in the California Current provide more context for

547 interpreting our results. Using an earlier version of the California Current Atlantis model,

548 Kaplan et al. (2010) forced moderate, acidification-driven declines on benthic

549 invertebrates, which caused declines in flatfish, small demersal sharks, and skates and

550 rays. These projected declines were consistent with ours, even though the meta-analysis

551 of Busch and McElhany (submitted) that informed the current analysis suggested that

552 seastars and brittlestars are less sensitive to acidification than was assumed by Kaplan et

553 al. (2010). Kaplan et al. (2010) also found indirect effects leading to increased canary

554 rockfish and the shallow miscellaneous fish group. These increases were not supported

555 by our analysis because we changed the functional group composition to better represent

556 groups susceptible to OA, which resulted in changes to the diet parameterization in these

557 groups. In a food web model with much simpler spatial structure and no oceanographic

558 forcing, Ainsworth et al. (2011) found very limited system-level effects of changing pH

559 on the northern portion of the California Current. In contrast to our results, cumulative

560 impacts of multiple stressors in their study were greater for the pelagic than demersal

561 components of the food web; this is likely because Ainsworth et al. (2011) assumed that

562 euphausiids were also sensitive to OA, which was not robustly supported by Busch and

563 McElhany (submitted).

564 Ocean acidification is not the only global change stressor affecting this ecosystem. King

565 et al. (2011) used conceptual models to forecast the effects of climate change on the

566 California Current, and focused primarily on changes in temperature, dissolved oxygen

567   and precipitation. They predicted that many demersal fish (such as Dover sole, sablefish,

568   and rockfish) may be buffered against ocean warming because they can move north or

569   into deeper water temperature refuges. They did not consider ocean acidification,

570   however, and our results suggest that OA may create vulnerability for demersal fish, even

571   relatively mobile ones, through erosion of their prey base. King et al. (2011) also

572   forecasted that warmer waters may support larger sardine populations, and since our

573   Atlantis results did not indicate indirect sensitivities to OA in the pelagic fish guild, this

574   may be an opportunity for a global change "winner" when combining the effects of

575   temperature and OA. Overall, further consideration of the joint effects of temperature,

576   ocean acidification and hypoxia are warranted within the California Current. King et al.

577   (2011) noted that some demersal fishes, such as Dover sole, may be able to take

578   advantage of expanding hypoxic zones on the continental shelf. Global modeling by

579   Barange et al. (Barange *et al.*, 2014) that includes temperature effects but omits

580   acidification suggests that some mid to high-latitude fisheries may benefit in the future,

581   and that primary production may increase in the northern portion of the California

582   Current. Stressors like OA, warming temperatures and low dissolved oxygen will likely

583   co-occur and interact (Reum *et al.*, 2014), and future Atlantis scenarios that attempt to

584   address these combined stressors will have to rely on experimental studies that examine

585   their cumulative effects on key species.

586   *Uncertainty, caveats, and gaps*

587   Projections of living marine resources under global change contain uncertainty stemming

588   from three sources: internal variability, model uncertainty (including parameter and

589   structural uncertainty), and scenario uncertainty (Cheung *et al.*, 2016). We have reduced

590   the effects of internal variability (e.g. interannual climate variation, interdecadal climate

591   regime shifts) by forcing Atlantis with a single representative year of oceanography and

592   biogeochemistry (2013 or 2063). Model parameter uncertainty is harder to address: large

593   numbers of input parameters within models such as Atlantis preclude some formal

594   quantification methods such as Bayesian or Monte Carlo approaches (Cheung et al.

595   2016). The computational expense and long run-times of Atlantis model simulations

596   present an additional challenge. In the future, parameter uncertainty may be addressed by

597   bounded parameterizations (Fulton *et al.*, 2011) that bracket stock productivities, an

598   approach that has been applied for an earlier version of the California Current Atlantis

599   model (Pacific Fishery Management Council & NMFS, 2014). Uncertainties stemming

600   from model structure can be understood via model inter-comparisons and skill

601   assessment (Payne *et al.*, 2015). Scenario uncertainty is likely to be the most important

602   factor for long term projections (Hawkins & Sutton, 2009) beyond the 2060s; we agree

603   with Cheung et al. (2016) that this is best captured using scenarios for not only emissions

604   and climate but also fishery development and management. Though our scenarios here

605   assume simple fixed fishing mortalities, global efforts (Merino *et al.*, 2010; Msangi *et al.*,

606   2013) and nascent local efforts (Kaplan *et al.*, 2012) to develop meaningful social-

607   economic scenarios offer promise in this respect.

608   Ecosystem model outcomes are fundamentally affected by modelers' assumptions and

609   decisions about input data, parameter development, and model structure (Link *et al.*,

610   2012). An assumption that is central to the present study is our parameterization of

611   sensitivity to pH. Despite a large body of experimental work (e.g., Busch and McElhany,

612   submitted), the sensitivities to pH for functional groups in our model are known with

613   very little precision. We expect the ranking of pH sensitivity to be generally robust, but

614   the scale of that sensitivity is hard to quantify in part because we are translating effects on

615   individuals under controlled experimental conditions to functional group-level effects in

616   the model. Further, we modeled pH sensitivity as reduced survival because that is the

617   most straightforward to implement and an approach similar to others' (Kaplan *et al.*,

618   2010; Griffith *et al.*, 2011; Weijerman *et al.*, 2015). However, meta-analyses suggest the

619   physiological effects of changing pH may also involve reproduction or growth (Kroeker

620   *et al.*, 2010). Modifying mortality rates as we have done here may be an appropriate

621   proxy in some cases but may over or under-represent the effect of changing pH on some

622   organisms. Using mortality rates to capture pH sensitivity has another limitation in our

623   Atlantis model; we are unable to project direct effects of OA that are positive (e.g., for

624   seagrasses), which limits the scope of our forecasts. However, we can, and did project

625   some positive indirect effects of future pH. Lastly, our results reflect the way we chose to

626   model the process of ocean acidification—by projecting pH, not aragonite or some other

627   calcium carbonate saturation state. Alternate ways of modeling OA may lead to different

628   conclusions about ecosystem and fishery effects.

629   Our California Current Atlantis model does not capture the dynamics of all functional

630   groups in the ecosystem—for example pandalid shrimp, market squid, and tuna

631   functional groups do not persist in our baseline 100-year model simulation. Therefore,

632   we cannot infer potential effects of OA on these components of the food web (or the

633   fisheries that target these groups). Two of the modeled fish groups (Petrale sole and

634   shallow small rockfish) persist in the baseline simulation and demonstrate strong indirect

635   sensitivity to pH, but these simulated groups may be less productive in the model than

636   they are in reality, and we may therefore overestimate their sensitivity to OA. This low

637   productivity is evident from calibration tests for some groups that suggest lower

638   sustainable yields than what has been estimated by stock assessments (see online material

639   Appendix B).

640   The caveats associated with ecosystem model projections are a good reminder of how

641   these results should be interpreted and used. Our findings about winners and losers in the

642   ecosystem, functional groups that are more or less sensitive to changing pH in the

643   California Current, and potential impacts to fisheries revenues provide a set of forecasts

644   that build upon previous findings and pave the way for hypotheses to guide future

645   modeling and experimental analysis. For example, in this study we summarized the

646   effects of changing pH at a coast-wide scale. We found limited effects at the coarse guild-

647   level but stronger effects when we looked at individual functional groups. Similarly,

648   aggregating across space likely had a smoothing effect that obscured more dramatic and

649   meaningful changes in particular locations. Spatial scale is particularly important when

650   considering the way that fishing communities interact with ocean ecosystems-- typically

651   with local knowledge and long histories of particular fishing grounds within reach of

652   home ports (St. Martin & Hall-Arber, 2008). Therefore, a key next step for this model is

653   to investigate how the effects of changing pH vary across space, and what that means for

654   place-based human communities, similar to a recent risk assessments for Alaskan fishing

655   regions (Mathis *et al.*, 2015) and larger US regions (Ekstrom *et al.*, 2015).

656   *Implications for management*

657   We can begin to understand cumulative impacts on large marine ecosystems by using

658   models that combine experimental studies, physical models, and food web models such

659　as the one presented here for the California Current. Describing and understanding effects

660　of global change on large marine ecosystems, including human communities, requires

661　integration of diverse methodologies and interdisciplinary teams (Hollowed *et al.*,

662　2013a). While this type of end-to-end model is not intended to make precise, tactical

663　forecasts for fisheries management, it can be used to identify risks to marine ecosystem

664　structure and function (Hollowed *et al.*, 2013b). Combined with information about the

665　adaptive capacity of human communities (Morzaria-Luna *et al.*, 2014; Mathis *et al.*,

666　2015), end-to-end models can inform risk assessments of human communities to global

667　change. Ocean acidification is occurring in the California Current, and our model

668　suggests the risks of changing pH are greatest for epibenthic invertebrates and demersal

669　fish, and the fisheries that target these groups. Models such as Atlantis can be used to

670　present broad alternatives for how ecosystems and populations may evolve under global

671　change, and our results provide strategic guidance to managers on the West Coast of the

672　U.S. that can be followed up with tactical simulation tests to identify robust management

673　strategies (Punt *et al.*, 2013).

674　**Acknowledgments**

680　**Supplementary Materials**

681　Appendix A. Atlantis model documentation.

682   Appendix B. Model sensitivity to fishing mortality rates.

683   Appendix C. Sensitivity of the pH effect of Benthic herbivorous grazers to the survival

684   scalar.

685
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